The Future Scenario of an Iconic Tree From the Brazilian Cerrado: Perspectives on *Eremanthus* Less. (Asteraceae) Conservation

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Abstract

Characterized as one of the largest biodiversity hotspots, the Cerrado ecoregion houses a wide variety of endemic species. Several threats, such as agricultural expansion and habitat fragmentation, put the species of the Cerrado ecosystems and biodiversity at risk. The genus *Eremanthus* is frequent in the Cerrado and suffers from intense anthropogenic pressure due to overexploitation mainly for the construction of fences and extraction of essential oil. Environmental suitability, of the Mid-Holocene, present and future (2070), were estimated for the genus in order to characterize the importance of the climate in the species distribution and to analyse the conservation status. The Species Distribution Modelling showed that most species of *Eremanthus* presented similarities between the environmental suitability of the present and the Mid-Holocene, enabling the identification of areas of environmental stability in OSL areas of campos rupestres. The species of the genus were classified as Endangered and Vulnerable according to IUCN criteria, presenting very reduced areas of environmental suitability projected in the future and a low percentage of species in Protected Areas, that may influence possible extinctions of species in the genus. The approaches in this study provide consistent subsidies to assist in conservation planning.

Introduction

The Cerrado, occupying the central portion of Brazil, part of Bolivia and Paraguay, is the largest neotropical savannah, whose biogeographical and morpho-climatic domain extends over about 2 million km^2. It is widely recognized as one of the largest biodiversity hotspots in the world due to its high species richness and index of endemism, with 44% of the total plant species and 80% of its woody plants exclusive to this environment (Lenthall et al. 1999; Klink and Machado 2005). The high environmental heterogeneity of the Cerrado favours the floristic diversity of plant communities, especially through the variety of soils (latosols, cambisols, gleis, hydromorphic laterite, litholic, sands quartzous, podzolic oxisols), climates and geomorphologies (Siqueira and Durigan 2007; Souza-Neto et al. 2016).

The dynamics of vegetation in the Cerrado is strongly influenced by wildfires, promoting the maintenance of various phytophysiognomies, with plants having different fire-resistance adaptations and fire dependence in their reproduction cycle (Simon et al. 2009; Simon and Pennington 2012; Rissi et al. 2017; Loram-Lourenço et al. 2020). The species richness in the Cerrado originates from the recent diversification of some endemic genera that occurred at approximately 10 Mya, coinciding with the expansion of C4 grasses during the Miocene (Simon et al. 2009).

The campos rupestres constituted one of the Cerrado physiognomies in this ecoregion, but recently it was recognized as a different and independent ecoregion and in this study Cerrado and campos rupestres will be treated as distinct phytophysiognomies, in agreement with recent ecoregion proposals (Colli-Silva et al. 2019; Morrone et al. 2022). Campos rupestres present remarkable topographic features with the presence of rock outcrops, promoting an endemic habitat for several species (Alves et al. 2014).

Despite the great importance of its biodiversity, the Cerrado suffers from intense environmental degradation. Currently, less than 20% of the Cerrado native vegetation is protected within reserves, with an estimated loss of 46% of its native vegetation; land use projections foresee intense deforestation in the coming decades (Strassburg et al. 2017; Terra et al. 2017). Environmental protection areas correspond to 6.5% of the Cerrado and only 3% of the natural vegetation is included in strictly protected areas in IUCN categories I to III (Françoso et al. 2015). There is an urgent need to preserve the Cerrado and campos rupestres biodiversity and scientific research towards this goal has in the last two decades contributing to the identification of biogeographic districts, assessment of land use and protected areas, spatial-temporal analysis of deforestation, climate studies, effects of fire on biodiversity dynamics, survey of threats and proposals to control them (Guisan et al. 2013; Françoso et al. 2015; Velazco et al. 2019; Colli et al. 2020; Fernandes et al. 2020).

The main threats to the Cerrado biodiversity are uncontrolled agricultural expansion that causes deforestation, habitat fragmentation and pollution of waterbodies with fertilizers and lime, intentional burning and replacement of Cerrado vegetation by exotic grasses to establish cattle pastures, which interfere in the natural ecosystem cycle (Klink and Machado 2005; Scarano et al. 2014) (Fig. 1). The campos rupestres are also under several and constant threats to biodiversity, such as mining, cattle overgrazing, invasion by exotic species, urban growth and native species overexploitation (Pena et al. 2017; Fernandes et al. 2020).

The OSL theory presents hypotheses regarding ecology, evolution and biological conservation in Old Stable Landscapes (OSL), which help to better understand areas that need greater biodiversity conservation (Mucina and Wardell-Johnson 2011). OSLs are landscapes that remained stable for millions of years and are characterized mainly by climatic stability and impoverished soils, all contributing to increased persistence of species lineages, maintenance of diversity and endemism, favouring the variability of fragmented population systems (Hopper 2009; Hopper et al. 2021; Silveira et al. 2021). The OSLs states that species in these environments tend to have limited seed dispersibility, which increases genetic divergence and allopatric speciation, high environmental specialization and phylogenetic niche conservatism (Hopper 2009; Mucina and Wardell-Johnson 2011; Hopper et al. 2016; Fiorini et al. 2019).

The Cerrado and campos rupestres harbour many endemic species of *Eremanthus* (Asteraceae, Vernonieae) and both phytophysiognomies are considered an important biodiversity hotspot, but the latter is also considered an important OSL area (Mucina and Wardell-Johnson 2011; Silveira et al. 2016, 2020; Loeuille et al. 2019; Hopper et al. 2021). *Eremanthus* is a neotropical genus of treelets or rarely shrubs, distributed almost exclusively in the Cerrado, with an important presence in the Espinhaço Range (MacLeish 1987; Loeuille et al. 2019; Alves and Loeuille 2021). They are easily recognizable and generally occur in large populations, being commonly known as “candeias” (loosely translated as lamps) due to their use as fuel (Scolforo et al. 2002; Macedo et al. 2020).

Plants produce several secondary metabolites that have properties of human interest, being potentially exploited by local populations and industries (Briskin 2000; Verma et al. 2012). The overexploitation of biochemical elements in plants has put several species at extinction risk, stimulating studies aimed at the conservation of these species (Rai et al. 2000; Ncube et al. 2011). This has been considered to be one of the major causes of species extinction along with other environmental disturbances, especially plants that are socioeconomically important (Rosser and Mainka 2002; Williams et al. 2014).

Eremanthus species are under constant threat due to intense anthropogenic overexploitation, mainly of *E. erythropappus* and *E. incanus*, which are used locally as fence posts and essential oil extraction by industries, being α-bisabolol the main component (Scolforo et al. 2002; Pádua et al. 2016). α-bisabolol, also known as levomenol, is a monocyclic sesquiterpene alcohol, firstly isolated from chamomile (*Matricaria chamomilla*) in 1951. It has anti-allergic, antibacterial, antiphlogistic, anti-irritant, antimycotic, dermatological, spasmodic and vermifugal properties, being widely used in the cosmetics and pharmaceutical industry.

Eremanthus erythropappus is an important example within the genus with studies that assess the threat and conservation situation and seek solutions to control the overexploitation of the species (Araújo et al. 2018; Pádua et al. 2021). Some studies propose to focus on genetic conservation of species through vegetative propagation methods, maintaining selected genotypes (Fonseca et al. 2021). Population distribution analyses show that over short distances populations are genetically similar and genetic assessments in species populations under anthropogenic influence help to identify priority conservation areas (Pádua et al. 2021). Integrating different methodologies can be very useful in conservation assessment (Peterson 2011; Grossi et al. 2017; Neves et al. 2018).

Some *Eremanthus* species are included in endangered species lists (e.g., Centro Nacional de Conservação da Flora (six species), Lista Oficial das Espécies Endêmicas da Flora Ameaçadas de Extinção do Estado da Bahia (two species) e Lista das Espécies Ameaçadas de Extinção da Flora no Estado de Minas Gerais (two species)). One of the most widely used threatened species classification system is the International Union for Conservation of Nature (IUCN) Red List, which presents categories and criteria that allow an objective evaluation of species extinction risk (IUCN Standards and Petitions Committee 2019). The two most frequently used metrics for assessing species according to the IUCN specifications are the Extent of Occurrence (EOO) and Area of Occupancy (AOO), with many studies using a variety of species distribution modelling methods to calculate EOO and AOO (Marcer et al. 2013; Fivaz and Gonseth 2014; Syfert et al. 2014; Visconti et al. 2016; Breiner et al. 2017; Marco et al. 2018; Moat et al. 2019; Kaky and Gilbert 2019), especially in cases where the data is scarce. The use of Species Distribution Modelling (SDM) in conservation status assessments needs to consider the Minimum Convex Polygon (MCP), which encompass all the predicted habitat areas, to estimate EOO and a grid size of 2 × 2 km to estimate AOO (IUCN Standards and Petitions Committee 2019).

The SDM methodology deals with the formulation of species distribution models presenting possible areas of positive environmental suitability, in agreement with the ecological niche, and based on the combination of current species distribution with environmental variables (Anderson et al. 2003; Elith et al. 2011; Godsoe et al. 2017). There are several applications of predictive species distribution modelling, such as in conservation research that address climate change with the projection of different chronologies, especially future ones (Stockwell and Peterson 2002; Anderson et al. 2003). These methods are used in several fields of biology, such as biogeographic studies, species protection and conservation programs, characterization of degraded areas, recognition of suitable areas for establishment of invasive species and delimitation of priority conservation areas (Araújo and Williams 2000; Peterson and Robins 2003; Engler et al. 2004; Ortega-Huerta and Peterson 2004; Peterson et al. 2006; Siqueira and Durigan 2007; Chen 2009).

Disregarding the interspecific relationships of species and evolutionary adaptations, performing an incomplete sampling of the niche, as well as errors in the data and variables inserted in carrying out the SDM can compromise the results obtained in the analysis and consequently the interpretations (Sinclair et al. 2010). Predictions for the future based on current data could over- or under-estimate species distributions due to uncertainty in projections on how species will respond to climate change and how this will affect the distribution ranges (Thuiller et al. 2008; Fitzpatrick and Hargrove 2009). Extrapolations for different time periods need to consider environmental differences and the equilibrium or not of the species with the environment, which can generate an interpretive risk due to the lack of information on distribution limiting factors and biotic interactions for the past and future (Dormann 2007; Elith and Leathwick 2009).

Another tool that can provide information about species conservation is Gap Analysis (GA), which is largely used in global or local scale and very useful in association with SDM in IUCN red-listing (Grossi et al. 2017). This methodology consists in identifying conservation gaps through the overlapping of data layers of geographical and biotic components, serving as a coarse filter for biodiversity protection (Scott et al. 1993). This analysis shows whether the species are included in Protected Areas (PAs), assessing species distributions according to existing areas under environmental protection policies, providing information about conservation coverage and guiding management actions (Jennings 2000).

This study aims to assess the conservation of all *Eremanthus* species, through the construction of environmental distribution models, application of the IUCN criteria based on records and SDM, and identification of PAs in the distribution models areas. The main questions we intend to answer are: 1) What are the estimated projected environmental suitability areas for the species over time (past, present and future)? 2) Is there a relationship between the Mid-Holocene climatic conditions and the current species distribution? 3) In what proportion are the species included in conservation units? 4) What is the extinction risk classification for the species according to the IUCN criteria? 5) What is the future of species conservation in the face of threats of environmental suitability reduction?

Materials And Methods

Data acquisition

The initial step was to obtain georeferenced data from all species of *Eremanthus* and create a record database. Most of the information was obtained from Benoit Loeuille's personal database, which contains high-quality taxonomic identification data, with support of records stored in the Species Link (http://splink.cria.org.br/) and Global Biodiversity Information Facility (GBIF - https://www.gbif.org/) online databases. After the compilation, the *Eremanthus* database was edited to remove unreliable records, keeping only data suitable for use in research, eliminating problems with misidentification, inaccuracy, records outside raster boundaries, more than one datapoint per pixel and duplicated records (Giannini et al. 2012). This process was carried out manually and with the clean functions ("clean_dupl", "clean_nas", "clean_uni") of the 'modleR' 0.0.0.9000 (Sánchez-Tapia et al. 2018) package in RStudio 1.3.1056 (RStudio Team 2020) with R 3.6.3 (R Core Team 2020), in a two-stage (automatic and manual) cleaning approach (Panter et al. 2020). Only 15 species (*E. capitatus* (Fig. 1b), *E. cinctus, E. crotonoides, E. elaeagnus* (Fig. 1d), *E. erythropappus, E. glomerulatus, E. goyazensis, E. incanus* (Fig. 1c), *E. mattogrossensis, E. mollis, E. polycephalus, E. reticulatus, E. rondoniensis, E. syncephalus, E. uniflorus*) were included in this study, because the other eight species (*E. arboreus, E. argenteus, E. auriculatus, E. brevifolius, E. hatschbachii, E. ovatifolius, E. praetermissus, E. veadeiroensis*) have less than 10 records in the database.

Species Distribution Modelling

SDM was performed using the 'modleR' package in RStudio. Brazil was the main study area, except for *E. cinctus*, *E. mattogrossensis* and *E. rondoniensis*, for which Brazil and Bolivia were used as base area, as there was suspicion from preliminary modelling tests that an area of suitability for *E. cinctus* could be present in Bolivia and because the other two species occur in both countries. Nineteen bioclimatic variables were obtained from the WorldClim version 1.4 database (Hijmans et al. 2005) with 2.5 minutes spatial resolution. The Global Climate Model (GCM) used was the Model for Interdisciplinary Research on Climate-Earth System Model (MIROC-ESM). To apply in the analysis, these variables were cropped through 'raster' package in RStudio using the previously described study area as base (Hijmans 2021).

The selection of the bioclimatic variables for modelling was performed with the 'modleR' package. Correlated variables were excluded, maintaining the bioclimatic variables Mean Diurnal Range (Mean of monthly (max temp – min temp)), Isothermality, Mean Temperature of Wettest Quarter, Mean Temperature of Warmest Quarter, Precipitation of Wettest Month, Precipitation Seasonality (Coefficient of Variation), Precipitation of Wettest Quarter, Precipitation of Warmest Quarter and Precipitation of Coldest Quarter. The modelling was carried out for the present (1960–1990) and projected to the past in the Mid-Holocene (~ 6000 years ago) and to the future in 2070 with all Representative Concentration Pathways (RCPs) scenarios (2.6, 4.5, 6.0 and 8.5), to visualize the range of suitable areas for species occupation through time. Past models had the purpose of elucidating the history of environmental suitability in *Eremanthus* from an OSL perspective and to identify possible influence on the current and future distributions. To maintain consistency with other analyses and avoid confusion, RCP 8.5 was maintained as a reference in the presentation of results and discussion. Maxent and Bioclim were the algorithms used for modelling and the models used in this study are an ensemble of both, based on models with True Skill Statistics (TSS) value above 0.7.

IUCN Red List assessment

The recommendations in the Guidelines for Application of IUCN Red List Categories and Criteria (IUCN Standards and Petitions Committee 2019) demonstrate how to carry out EOO and AOO calculations, including cases of spatially predicted sites. Furthermore, SDM models need to be binarized through a threshold value before these calculations. The thresholds must be properly established because they directly affect the coverage of suitable habitats in the binarized models and, consequently, the species status assessment (Liu et al. 2005, 2016).

The species classification method for IUCN red-listing followed the parameters established by the IUCN Red List Categories and Criteria Version 3.1 (IUCN 2001, 2012) and Guidelines for Application of IUCN Red List Categories and Criteria Version 14 (IUCN Standards and Petitions Committee 2019). The species were submitted to criterion B, which refers to the limitation of geographic distribution, and to subcriterion (b), referring to continuous decline. No analyses were carried out to enable the classification of species in subcriteria (a) and (c), which deal with severely fragmented populations and extreme fluctuations in populations, respectively. According to the IUCN provisions, to determine that a species is fully classified in criterion B, the assessed species must also meet the requirements of at least two of the three previously mentioned subcriteria. Therefore, the results of the assessment of *Eremanthus* species based on the IUCN criteria are presented in a preliminary way. Notwithstanding, in the face of worsening imminent environmental threats worldwide, this study presents consistent and important preliminary results that will serve as basis for a classification that completely fulfils the IUCN Red List requirements.

The letters “f”, “h”, “l”, “p”, “r” and “t”, when mentioned together with EOO and AOO, are abbreviations for “future”, “hull” (referring to convex hull/MCP), “loss”, “present”, “records” and “total” (referring to total area), respectively. To evaluate *Eremanthus* species according to the IUCN specifications for criterion B, individual records were used to calculate EOOr (criterion B1), through MCP, and AOOr (criterion B2), using the 2 × 2 km (4 km^2) reference scale for grid size. EOO and AOO of SDM models of the present (EOOp and AOOp) and of the future with RCP 8.5 (EOOf and AOOf) were calculated, as well as their respective values within the MCP (EOOph, AOOph, EOOfh and AOOfh), in order to identify a possible decline of a species in the projections. To perform such calculations, SDM models were binarized (i.e., areas with environmental suitability received a value of 1 and areas without environmental suitability received a 0 value) by obtaining the threshold values when the Minimal Predicted Area (MPA) with 90% of the species records was applied, in order to avoid any possible remaining incorrect records and ensure the reliability of the records in the analysis. With these binary models representing the potential habitat area, the area of occupied habitat was estimated and EOOp, AOOp, EOOf, AOOf, EOOph, AOOph, EOOfh and AOOfh were calculated. These procedures were carried out in the R packages ‘ecospat’ (Broennimann et al. 2020) and ‘red’ (Cardoso 2020).

Gap Analysis

The previously generated binarized models were used as basis for GA calculation. This enables greater parameterization of the analysis and higher fidelity in result comparison, in addition to ensuring more reliable results, as the binary models follow a calculated threshold. The anthropized areas (BDiA 2020) were removed from the binarized models to avoid inserting areas where the species certainly do not occur, i.e., only suitable areas with anthropogenic absence were used in the analysis. The layers resulting from this process were overlapped with the PAs (ICMBio 2020), and PAs occurring in suitable areas were identified and extracted. The percentage of protected areas within the environmental suitability area for each species was then calculated. The next step was to identify which species are present within PAs and calculate how many records represent the presence of the species in these areas. All these procedures were performed in the software QGIS 3.12.0 (QGIS Development Team 2020).

Cartographical procedures

E. erythropappus was selected as an example to cartographically represent the results obtained here, as it is the better known and exploited *Eremanthus* species. Maps representing the results for other *Eremanthus* species are available in the Online Resource 1–45. Maps were designed using the software QGIS 3.12.0, using the data generated in the previous analyses.

Results

SDMs and environmental suitability

The models resulting from the SDM showed satisfactory results. With the exception of *Eremanthus capitatus* and *E. crotonoides*, the environmental suitability of the species in the models corresponding to the Mid-Holocene period showed similar and reduced areas compared to the SDM environmental suitability results for the present (see electronic supplementary material). *E. capitatus* showed a more extensive area of suitability in the past when compared to the present, especially on the eastern Brazilian coast between the states of Bahia and Rio de Janeiro (Online Resource 1, 2). Similarly, when compared to the models based upon data for the present, *E. crotonoides* demonstrated to have a greater suitability on the coast from north-eastern São Paulo to southern Bahia and also on the northern portion of the state of São Paulo in the Mid-Holocene period (Online Resource 7, 8).

The SDM results for the present were consistent with the records, showing wider areas of suitability in relation to the current distribution of the species and in agreement with the Cerrado. The Espinhaço Range was the region which more frequently appeared in the models as an area conducive to the establishment of the species, especially the Espinhaço Meridional, including for *Eremanthus cinctus* (Online Resource 5), *E. goyazensis* (Online Resource 20), *E. mattogrossensis* (Online Resource 26), *E. mollis* (Online Resource 29) and *E. uniflorus* (Online Resource 44), which currently do not have records in this geological formation. The Eastern Cordillera in Bolivia was an important present area of suitability in the models of *E. cinctus*, *E. mattogrossensis* and *E. rondoniensis*, with the exception of *E. cinctus* in the future and *E. mattogrossensis* in Mid-Holocene simulations, which did not show significant suitability in that region (Online Resource 4–6, 25–27, 37–39). *E. mattogrossensis* showed a large variation in SDM results in the three time periods, presenting disjunct areas in the Mid-Holocene in the Espinhaço Range, Planalto dos Guimarães, surroundings of Chapada dos Parecis and Depressão da Amazônia Meridional, a wider suitability in the present, and high reduction in suitability estimated for the future (Online Resource 25–27).

In relation to the results presented by the future SDM models, a great decrease in the environmental suitability area was observed for all species in all RCP scenarios when compared to the present models. The loss of suitability between models at the different RCP levels was relatively similar and with a gradual increase from the RCP 2.6 level (more optimistic scenario) to the RCP 8.5 level (more pessimistic scenario). Almost all species showed decrease of suitability area to a very reduced region between the states of Minas Gerais, Rio de Janeiro and São Paulo, especially in areas of Serra da Mantiqueira and Serra do Mar (see electronic supplementary material). *E. cinctus* (Online Resource 6), *E. goyazensis* (Online Resource 21), *E. mollis* (Online Resource 30) and *E. uniflorus* (Online Resource 45) show a trend to disappear from the current distribution areas, with a more critical situation for the latter, which will practically lose the entire adequacy area where current records are located. The Cordillera Oriental showed a high level of suitability in the future projection of *E. rondoniensis*, while the areas of suitability in Brazil were significantly reduced (Online Resource 39). The future projection of *E. capitatus* showed a great extent of adequacy area, however, with a low adequacy index for the most part (Online Resource 3).

Eremanthus erythropappus presented well-marked and similar areas of environmental suitability for the Mid-Holocene and the present (Figs. 2, 3). In the past, the species distribution estimative was restricted to Espinhaço Meridional, Serra da Mantiqueira, Serra do Mar and Serra da Canastra, while the present model highlighted the same regions with a small increase in the area of environmental suitability towards Brasília. Projections for the future estimate a drastic reduction in the suitability area of about 75% compared to the present, with restriction to the northeast portion of São Paulo, Serra da Mantiqueira and Serra do Mar (Fig. 4, Table 1).

Table 1
Percentage values found for records in protected areas (Records PAs), protected areas in suitability area for present and future models (Present PAs and Future PAs) and suitability area loss estimated for total area and protected areas (TAs Loss and PAs Loss) related to SDM models. PA = Protected area; TA = Total area

Species	Records PAs	Present PAs	Future PAs	TAs Loss	PAs Loss
E. capitatus	21%	14%	28%	89%	79%
E. cinctus	8%	15%	60%	96%	86%
E. crotonoides	26%	20%	61%	82%	48%
E. elaeagnus	35%	19%	47%	75%	40%
E. erythropappus	28%	27%	68%	74%	38%
E. glomerulatus	41%	16%	49%	91%	74%
E. goyazensis	37%	17%	42%	92%	81%
E. incanus	26%	18%	54%	86%	60%
E. mattogrossensis	22%	12%	41%	97%	92%
E. mollis	36%	17%	56%	92%	77%
E. polycephalus	29%	12%	38%	83%	51%
E. reticulatus	25%	22%	37%	53%	21%
E. rondoniensis	26%	12%	25%	51%	2%
E. syncephalus	33%	26%	47%	68%	43%
E. uniflorus	72%	22%	34%	95%	93%

Gap Analysis: Records and PAs

Present

With the exception of *E. uniflorus*, all other species presented less than 50% of their records within PAs (Table 1). The highest and lowest percentage of records in PAs were found in *E. uniflorus* (72%) and *E. cinctus* (8%), respectively. All species showed low percentages of PAs in areas of suitability, with values between 12% (*E. mattogrossensis*) and 27% (*E. erythropappus*) and the majority presenting values below 25%. The average percentage of records in PAs was 31% and the average percentage of suitability areas contained in PAs was 18% (Table 1).

Future

The results presented here reflect a stationary condition of the PAs. In view of changes in circumscription of PAs caused by climate change and public policies, the future GA values can be different. *Eremanthus* *cinctus*, *E. crotonoides*, *E. erythropappus*, *E. incanus* and *E. mollis* showed percentage values of PAs in suitability areas greater than 50% (60%, 61%, 68%, 54% and 56%, respectively). The other species showed values between 25% (*E. rondoniensis*) and 49% (*E. glomerulatus*), with an average percentage of 46%. The projected percentages of suitability area loss and PA loss in relation to suitability areas were evaluated. The lowest and highest percentages of suitability area loss were 51% for *E. rondoniensis* and 97% for *E. mattogrossensis*, with an average value of 82% among all species. *Eremanthus uniflorus* and *E. rondoniensis* presented the highest and lowest percentage values of PA loss with 93% and 2%, respectively, and the average among all species was 59% (Table 1).

EOO, AOO and IUCN red listing

Consistent values of EOO and AOO were obtained in all situations defined for this study. The values found for AOOr were sufficient to fit the species in the requirements of IUCN criterion B (Table 2). The EOOp, AOOp, EOOf, AOOf, EOOph, AOOph, EOOfh and AOOfh results allowed us to identify a projected decline in EOO and AOO, due to the difference between present and future values. All species presented considerable EOO and AOO losses. The projections show an average percentage of total area EOO and AOO loss (EOOtl and AOOtl) of 60% and 83%, respectively, and of 71% and 89% for the area belonging to MCP records (EOOhl and AOOhl), respectively.

Table 2

Extent of Occurrence and Area of Occupancy of the records in km^2 (EOOr and AOOr), proposed IUCN categories (IUCN Category) and projected loss percentages of the Extent of Occurrence and Area of Occupancy, considering the total area (EOOtl and AOOtl) and the records Minimum Convex Polygon (EOOhl and AOOhl). EOO = Extent of Occurrence; AOO = Area of Occupancy; MCP = Minimum Convex Polygon, VU = Vulnerable; EN = Endangered; h = convex hull (MCP); l = loss percentage; r = records; t = total area

Species	EOOr	AOOr	IUCN Category	EOOtl	AOOtl	EOOhl	AOOhl
E. capitatus	885,507 km^2	616 km^2	VU	30%	89%	65%	94%
E. cinctus	360,580 km^2	48 km^2	EN	94%	92%	100%	100%
E. crotonoides	519,587 km^2	516 km^2	VU	75%	77%	75%	90%
E. elaeagnus	125,365 km^2	204 km^2	EN	56%	85%	77%	90%
E. erythropappus	690,176 km^2	584 km^2	VU	50%	81%	62%	85%
E. glomerulatus	777,541 km^2	612 km^2	VU	59%	87%	66%	91%
E. goyazensis	357,086 km^2	296 km^2	EN	74%	80%	96%	96%
E. incanus	439,893 km^2	508 km^2	VU	57%	90%	66%	93%
E. mattogrossensis	1,692,804 km^2	312 km^2	EN	49%	90%	69%	95%
E. mollis	202,975 km^2	132 km^2	EN	81%	85%	98%	98%
E. polycephalus	92,945 km^2	140 km^2	EN	48%	88%	51%	92%
E. reticulatus	104,652 km^2	64 km^2	EN	35%	65%	34%	53%
E. rondoniensis	90,008 km^2	72 km^2	EN	61%	59%	65%	79%
E. syncephalus	168,166 km^2	124 km^2	EN	35%	81%	39%	87%
E. uniflorus	32,071 km^2	40 km^2	EN	98%	91%	100%	100%

When it comes to EOOf and AOOf, only *E. uniflorus* fits IUCN criterion B parameters, however, the situation considerably changes when EOOfh and AOOfh are used. In this case, *E. cinctus*, *E. goyazensis*, *E. mollis* and *E. uniflorus* fit the geographic limitation criterion for both measurements, while *E. elaeagnus*, *E. polycephalus* and *E. syncephalus* are classified under the same criterion only with AOOfh values. In this situation, *E. cinctus* and *E. uniflorus* are the most critical cases, with total absence of these two species within the areas of the convex hull of records in future estimates.

EOOr, EOOp, AOOp, EOOph and AOOph results were not significant for classification under IUCN criterion B. Thus, the species of the *Eremanthus* classified in IUCN criterion B2b(i,ii), considering AOOr results and the projected EOO and AOO reductions were *E. capitatus*, *E. crotonoides*, *E. erythropappus*, *E. glomerulatus* and *E. incanus* in the Vulnerable (VU) category and *E. cinctus*, *E. elaeagnus*, *E. goyazensis*, *E. mattogrossensis*, *E. mollis*, *E. polycephalus*, *E. reticulatus*, *E. rondoniensis*, *E. syncephalus* and *E. uniflorus* in the Endangered (EN) category (Table 2). Currently, IUCN presents a conservation status classification for *E. cinctus, E. elaeagnus*, *E. erythropappus E. glomerulatus*, *E. goyazensis*, *E. incanus*, *E. mattogrossensis* and *E. uniflorus* in the Least Concern (LC) category, for *E. auriculatus* and *E. praetermissus* in the Vulnerable (VU) category, for *E. argenteus*, *E. leucodendron* and *E. veadeiroensis* in the Endangered (EN) category and for *E. brevifolius* and *E. ovatifolius* in the Critically Endangered (CR) category. CNCFlora classifies *E. capitatus* and *E. crotonoides* as LC, *E. argenteus* and *E. leucodendron* as EN and *E. polycephalus* and *E. seidelii* (= *E. elaeagnus*) as VU (Martinelli and Moraes 2013).

Discussion

The application of SDM methods facilitates understanding the relationship between species geographical distribution and ecological niche, considering biotic, abiotic and distribution factors (Peterson et al. 2011). The use of SDM is recommended in studies proposing conservation-oriented decision making, such as ours, contributing to direct actions (Guisan et al. 2013).

The similarities found between Mid-Holocene palaeomodels and models for the present in the SDM results show a pattern of environmental stability in several areas of the Espinhaço Range (e.g., Diamantina Plateau and Serra do Cipó), Serra da Canastra and mountainous regions from Goiás, which corroborate to the OSLs and reinforce the importance of the environmental stability during the process of contractions and expansions of high altitude vegetation (Barbosa 2011; Bitencourt and Rapini 2013; Barres et al. 2019; Rapini et al. 2021). Several studies have shown the importance of Espinhaço Meridional as the main area of endemism and centre of origin for several campos rupestres plant species in the Espinhaço Range, further corroborating the importance of this mountainous formation as shown in *Eremanthus* SDM (Echternacht et al. 2011; Inglis and Cavalcanti 2018; Alves and Loeuille 2021). The occurrence of several *Eremanthus* species in high altitude campos rupestres areas is likely due to climatic fluctuations during the Holocene and previous geological periods (Silva et al. 2020). Expansions and contractions of specific vegetation types resulted in the establishment of campos rupestres as one of the typical altitude vegetation in Brazil (Barbosa 2011).

The distribution of *Eremanthus* species could have been influenced by the warm and dry climates that predominated in the Mid-Holocene, with the past SDM presenting suitability conditions similar to the present ones (Steig 1999; Behling 2002; Wanner et al. 2008; Bitencourt and Rapini 2013). Our results are thus consistent with the OSL theory, in which the presence of climatically stable areas for long periods of time promoted genetic isolation of *Eremanthus* populations and consequent speciation, favouring endemism (Mucina and Wardell-Johnson 2011; Hopper et al. 2016; Silveira et al. 2016; Fiorini et al. 2019). Other studies using SDM with other plant families, such as the locally diverse Velloziaceae and Bromeliaceae, obtained similar results, giving further evidence of the stability of OSL areas, especially in campos rupestres (Hmeljevski et al. 2017; Fiorini et al. 2019; Vidal et al. 2019; Cortez et al. 2020).

Considering the current occurrence records, the high density of botanical collections from the Espinhaço Range and the SDM simulations, it is unlikely that *E. cinctus* (Online Resource 4, 5), *E. goyazensis* (Online Resource 19, 20), *E. mattogrossensis* (Online Resource 25, 26), *E. mollis* (Online Resource 28, 29) and *E. uniflorus* (Online Resource 43, 44) have occupied this mountain range in the past, but unidentified biotic and/or abiotic dispersion barriers may have kept the species away from this area (Alves and Loeuille 2021). The environmental suitability of the Espinhaço Range for *E. elaeagnus* (Online Resource 10, 11), *E. incanus* (Online Resource 22, 23), *E. polycephalus* (Online Resource 31, 32), *E. reticulatus* (Online Resource 34, 35) and *E. syncephalus* (Online Resource 40, 41) occurred nearly exclusively during the Mid-Holocene, posteriorly advancing through the Brasília Arch (mountainous formations extending from the southern limit of the Espinhaço Range, passing through Serra da Canastra and heading towards Chapada dos Veadeiros). Few records of *E. incanus*, *E. reticulatus* and *E. syncephalus* are found in the Brasília Arch, mostly concentrated in the Espinhaço Meridional, suggesting a recent occupation of the Brasília Arch. According to the simulations, we can assume that the climatic changes after the Mid-Holocene increased the environmental suitability for *E. mattogrossensis* (Online Resource 25–27), allowing a connection between previously separated areas of suitability and generating favourable conditions for range expansion (Steig 1999; Behling 2002; Wanner et al. 2008).

The SDM models for present environmental suitability showed that high elevation regions corresponding to the Espinhaço Range campos rupestres are important areas for *Eremanthus*, even though species do not have current records in these locations. The Espinhaço Meridional presents higher environmental suitability in comparison to the Espinhaço Septentrional and Chapada Diamantina. The Brasília Arch also is an important area of suitability, as it houses records for some species and presents potential conditions for establishment of *Eremanthus* species. Planalto da Diamantina and Serra do Cipó, widely recognized as areas of intense research, hosting national parks focused on campos rupestres conservation, are other important regions highlighted by the modelling (Rapini et al. 2008; Alves and Loeuille 2021).

The GA and SDM results show that strong anthropogenic presence affect most areas of suitability in the SDM models (see electronic supplementary material). Most species of *Eremanthus* are distributed in small areas immersed in a high demographic density matrix, limiting the areas where they can establish and contributing to the intensification of population restriction (Mcdonald et al. 2008, 2009).

Conservation units constitute a very low percentage in areas of suitability for *Eremanthus*, increasing the possibility of species disappearing from the natural environment as anthropogenic occupation becomes more intense in unprotected areas (Rapini et al. 2008; Mcdonald et al. 2009). Fragmented areas with limited environmental suitability and threatened by anthropogenic activities (e.g., mining, fires, agriculture, livestock, urban expansion, exotic and invasive species, extraction of non-timber products) is also a problem to other groups, such as *Espeletia* (Asteraceae) that occur in mountainous Andean areas in the Páramo heterogeneous habitats (Valencia et al. 2020).

Among the species studied here, *Eremanthus erythropappus* is the one subjected to greater anthropogenic threats, due to indiscriminate wood extraction, being the subject of several conservation studies (Scolforo et al. 2002; Pádua et al. 2016) (Fig. 1e). *E. erythropappus* is commonly found in soils with high heavy metal concentrations, with implications to implementation of revegetation measures, in addition to sustainable management projects (Machado et al. 2013; Araújo et al. 2018). Population genetics studies are important to understand microevolutionary processes that can influence in the conservation of species like *E. erythropappus*, informing how populations should be managed. Studies of functional traits can show how the environment promotes variation in the species morphology (Borges et al. 2018; Rocha et al. 2020a, b). A concerted effort between the government, the private sector and the society is needed for the preservation of this species, which otherwise will likely disappear from nature (Carvalho et al. 2019).

The future projections show a dire scenario. The expected suitability areas for *Eremanthus* are very small, and some species will likely become extinct in the natural environment, such as *E. uniflorus* (Online Resource 45). Additionally, these areas present a much lower potential for suitability when considering the GA results, further aggravating the situation, as PAs might not be effective to protect species, due to the reduced percentage of records in them (Oliveira et al. 2017). It is likely that many species of *Eremanthus* will not be able to reach areas of future suitability and establish in the areas identified by GA, as these favourable suitability areas are in regions with high levels of anthropogenic activity and few preserved areas (Mcdonald et al. 2009). Given that our results consider the current situation of anthropogenic areas and conservation units in the future projections, the conservation situation of *Eremanthus* species is expected to become more critical in the coming decades. A common issue for species likely to be subjected to future distribution restrictions is AOO volatility, i.e., differences in species distribution along time in restricted and environmentally impacted areas cause an oscillation of the future estimated AOO (Marco et al. 2018).

Our study presents similar results to those of Carvalho et al. (2019), especially in the drastic reduction of projected future suitability areas, requiring immediate conservation actions, as they show a restriction of the distribution to the regions of Serra da Mantiqueira and Serra do Mar, and disappearance in several areas where it is currently distributed (Figs. 3, 4). We also obtained similar results to those of Bitencourt et al. (2016), with the majority of the suitability areas for campos rupestres in the Espinhaço Range but also in other areas such as Serra da Canastra (Minas Gerais state) and Chapada dos Veadeiros (Goiás state), projection of great loss of suitability area (including the few PAs of the Espinhaço Range) with the campos rupestres almost exclusive in the Espinhaço Meridional (barely present in the northern and outside of the Espinhaço Range) and a high potential of species extinction in campos rupestres due to habitat loss. A small number of endemic species is protected by PAs and many of these areas may become less effective due to climate change, therefore, conservation actions need to consider the representativeness and ecology of the species (Bitencourt et al. 2016). The presence of *Eremanthus* in PAs is also low and can be affected by the climate change in the coming decades.

When estimating areas of suitability using quantitative values, SDM serves as an objective resource in IUCN assessments that aim to understand the relationship of the species with the environment (Sangermano and Eastman 2012). The integrative application of SDM, GA and IUCN red listing allows the visualization of the current distribution of the species and their future behaviour in face of environmental conditions, in addition to contributing to conservation management by identifying the percentage of PAs within EOO and AOO (Marcer et al. 2013). These results can serve as a basis for planning conservation strategies with greater preparation and effectiveness, especially when it comes to developing countries where research is scarce (Fivaz and Gonseth 2014). Reliable results are obtained when measurements of EOO and AOO are performed using SDM models in a careful approach (Kaky and Gilbert 2019).

The use of SDM as a tool for classifying *Eremanthus* species in IUCN criterion B2b(i,ii) was effective, especially regarding the assessment of species spatial distribution and the future behaviour of EOO and AOO in relation to extinction risks (Kaky and Gilbert 2019). SDM showed a projected decline for EOO and AOO, both being essential components for IUCN classification (IUCN Standards and Petitions Committee 2019). The results showed that AOOr values were essential to classify *Eremanthus* species in threatened species lists, as none of the EOOr results met IUCN requirements (Kaky and Gilbert 2019). When comparing EOOph, AOOph, EOOfh and AOOfh with EOOp, AOOp, EOOf and AOOf it is evident that the manner in which the MCP of the SDM models is delimited greatly influences results, when considering the criterion B parameters (Fivaz and Gonseth 2014).

Although our methodological approaches were positively integrated in the results, some issues need to be noted. SDM can generate a wide range of models with different environmental suitability probabilities, therefore, it must be carefully prepared and evaluated, especially regarding the choice of environmental layers, which should consider the actual condition of the species (Fivaz and Gonseth 2014; IUCN Standards and Petitions Committee 2019). Depending on the level of the RCP used for the future projections, the generated models can result in conflicting environmental suitability conditions that can directly influence other analyses (Moat et al. 2019; Kaky and Gilbert 2019). The use of different algorithms can also influence research results and interpretations and should be chosen appropriately (Elith and Leathwick 2009). The two-stage cleaning approach of database records is essential for result credibility and accuracy, especially in species extinction risk assessment (Panter et al. 2020). The records should be properly filtered to eliminate possible errors, as the geographic location of the species directly influences MCP, EOO and AOO values and consequently the fitting of the species in IUCN red list categories (Fivaz and Gonseth 2014). Additionally, the effects of species sampling on SDM performance and accuracy and the use of statistical evaluation criteria for the models should be considered (Stockwell and Peterson 2002; Allouche et al. 2006; Wisz et al. 2008).

The absence of data in the SDM that portray the species biotic factors compromises the real prospects of how species can overcome environmental threats, especially in future estimates as the effects and constraints of these biotic relationships can be ignored (Elith and Leathwick 2009; Sinclair et al. 2010). Populations and species are subject to the consequences of natural selection, contributing to the reduction of the risk of extinction of species as they can adapt to environmental changes even in scenarios of accelerated modification (Etterson and Shaw 2013; Fox et al. 2019; Bemmels and Anderson 2019). SDM models may overestimate environmental losses and species extinctions by not considering potential genetic adaptations in response to environmental changes, and incorporating genomic data into the analysis may increase the reliability of the results (Razgour et al. 2019). Inclusion of approaches involving evolutionary processes and local adaptations of species in the SDM demonstrate that the risks of environmental vulnerability presented in the models are reduced, which contribute significantly for a better species dynamic interpretation (Bush et al. 2016; Peterson et al. 2019; Chen et al. 2020). The factors mentioned above, along with other variables such as migration, genetic drift and population dynamics, contribute to the change in species distributions of future predictions, since these factors are dynamic, unpredictable and can be incorporated into the SDM, generating different interpretations (Bush et al. 2016; Razgour et al. 2019).

It is important to highlight that anthropogenic threats continue to intensify in Cerrado and campos rupestres areas, mainly due to mining, which drastically changes the natural landscape by modifying the relief, removing soil and vegetation, the use of alien grasses for pasture and deforestation caused by agriculture expansion (Ratter et al. 1997; Pivello et al. 1999; Pena et al. 2017). Some habitat recovery initiatives have been implemented over the years, however, restoring the natural conditions of botanical communities is difficult and further impaired by the threat of ruderal invasive species (Silveira et al. 2016). OSLs are extremely important for global biodiversity and the Brazilian savannas are especially important in this context: they harbour thousands of endemic species resulting from a long historical process and are in serious risk of disappearing in the coming decades due to slowness of conservation actions (Mucina and Wardell-Johnson 2011; Hopper et al. 2016; Silveira et al. 2016). Few protection areas are located in OSLs areas in Brazil and the low representation of endangered species in these areas reinforce the idea that PAs are not effective in protecting biodiversity (Françoso et al. 2015; Neves et al. 2018).

The results presented here are positive from the perspective of their applicability as a scientific contribution and, along with previous research, reinforces the pertinence of SDM for application of IUCN Red List Criteria (Marcer et al. 2013; Fivaz and Gonseth 2014; Syfert et al. 2014; Marco et al. 2018; Moat et al. 2019; Kaky and Gilbert 2019). Future study that investigates the populational dynamics of *Eremanthus* may be the path to complete the necessary requirements for including species of the genus in IUCN Red List Criteria. The application of SDM in paleoclimates anterior to the Mid-Holocene (e.g., Last

Glacial Maximum and Last Inter-Glacial) can bring important information about distribution cycles in the genus and the possible implications for present and future species distribution.

Conclusions

Due to the Mid-Holocene climatic changes, and possibly from previous periods, the campos rupestres and Cerrado areas underwent expansion and contraction processes that probably resulted in changes in the geographic distribution of *Eremanthus* species. Present and future suitability areas found in the SDM allowed to identify regions for species establishment, however, a significant part of these areas has some degree of anthropogenic interference. As a consequence, a small percentage of the suitability areas is actually available for species occupation, with an even smaller fraction of these areas within PAs, which explains the current low proportion of species records in conservation units. The future prospects dire in relation to species sustainability in nature. Thus, classifying threatened species using the IUCN Red List criteria, even if partially, is essential for the elaboration of strategies for preparation and application of conservation-oriented policies and prevention of environmental damage. The Espinhaço Range, core area of the *Eremanthus* distribution, harbour several threatened plant groups in an important physiognomy that needs to be better scientifically understood for preservation purposes. The results obtained through integration of different methodologies provide the basic framework for their application in conservation models.

Electronic Supplementary Material

Maps representing the results of the species distribution modelling and gap analysis for all *Eremanthus* species.

Declarations

Conflict of interest: The authors declare that they have no conflict of interest.

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Data availability: All data generated or analysed during this study are included in this published article (and its supplementary information files).

Author Contributions: All authors made substantial contributions to the conception and design of the work; the acquisition, analysis, and interpretation of data; drafted the work and revised it critically for important intellectual content; approved the version to be published; and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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Figures

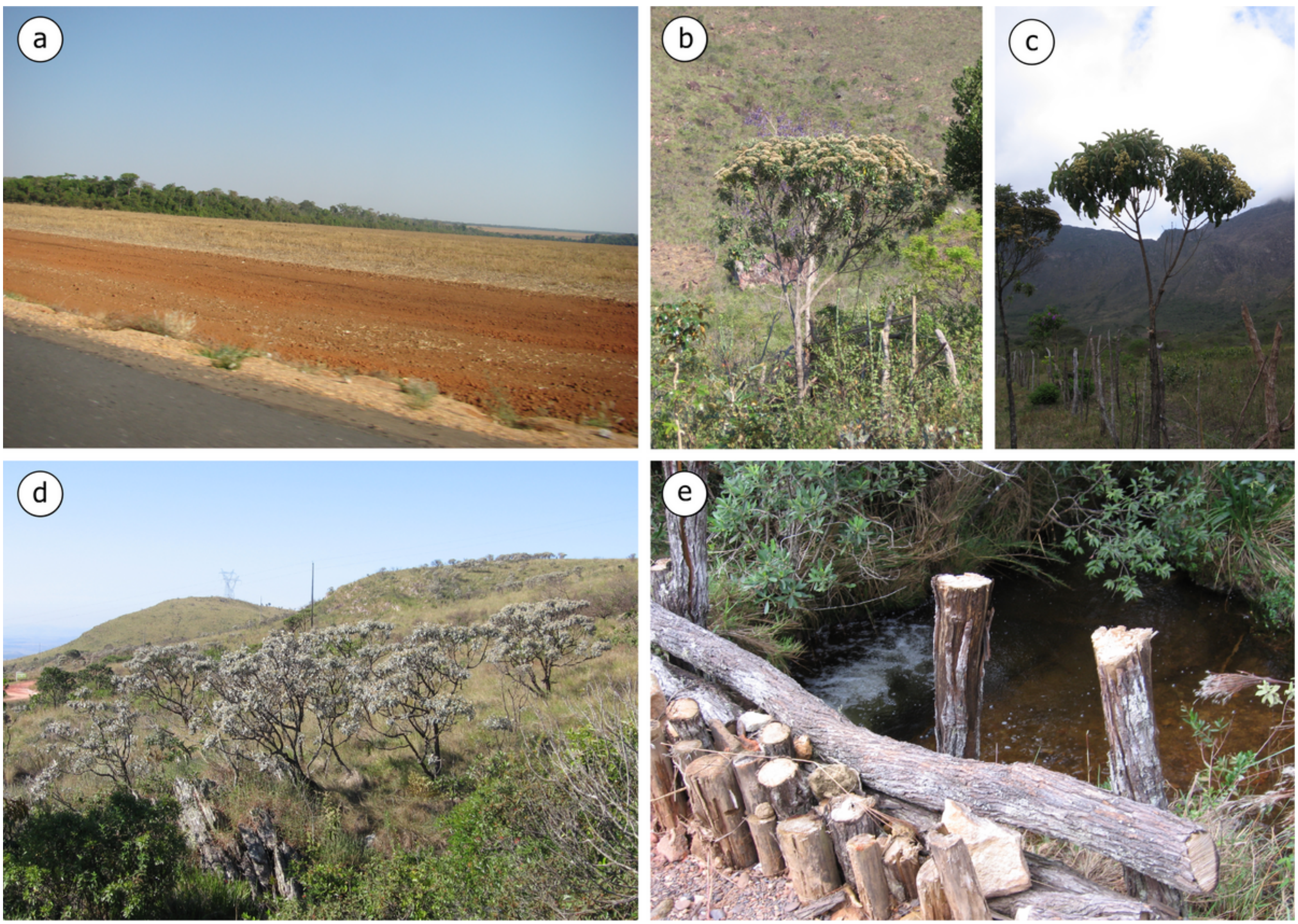

Figure 1

(**a**) Large deforested area where a population of *E. rondoniensis* was present at least until 2004; (**b**) *E. capitatus*; (**c**) *E. incanus*; (**d**) *E. elaeagnus*; (**e**) *E. erythropappus* wood being used as bridge structure

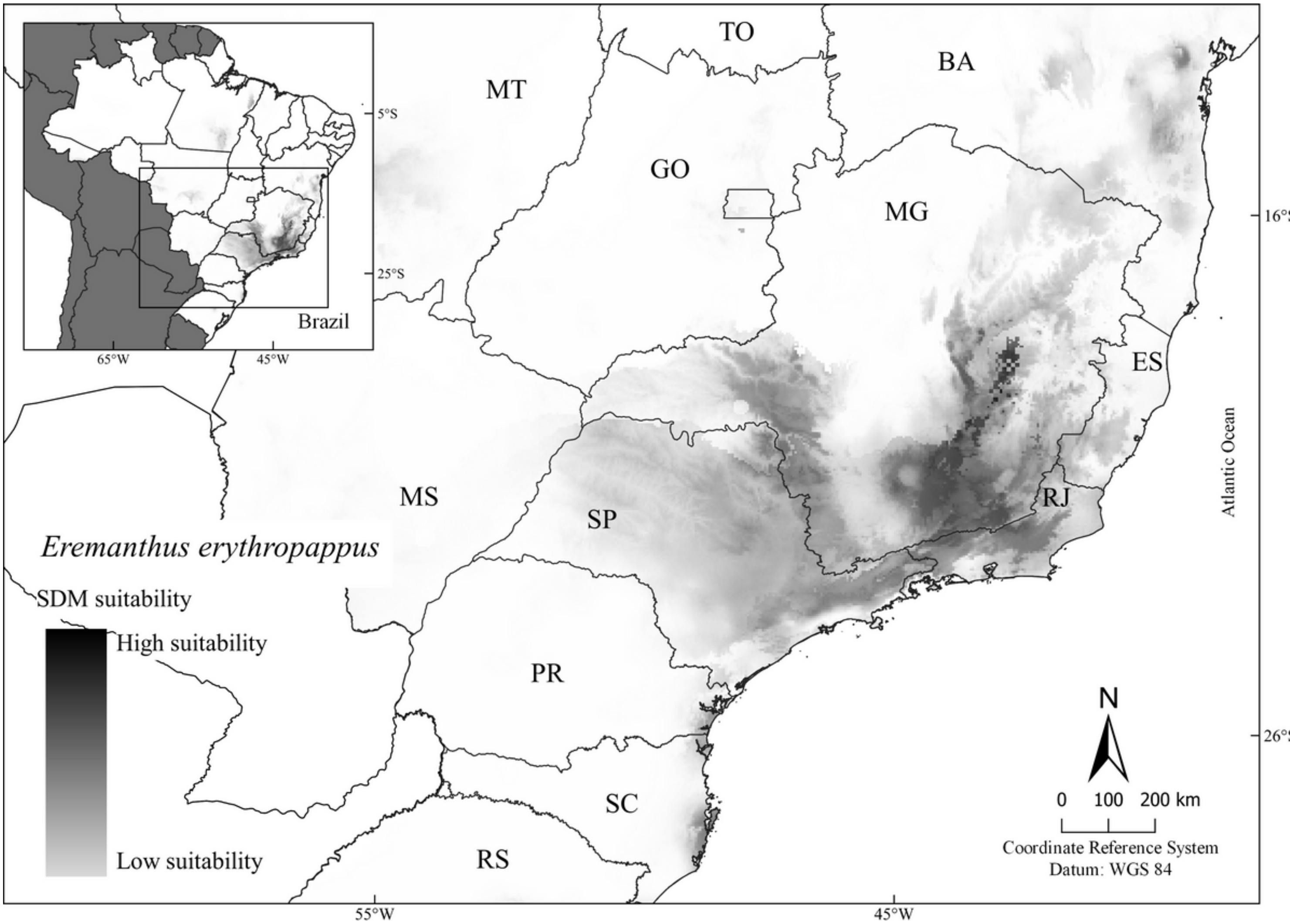

Figure 2

E. erythropappus Mid-Holocene suitability areas. Grey-scale areas show the environmental suitability of the Species Distribution Modelling (SDM), with intensity corresponding to the map scale. Darker areas indicate higher environmental suitability. Brazilian states: BA – Bahia; ES – Espírito Santo; GO – Goiás; MG – Minas Gerais; MS – Mato Grosso do Sul; MT – Mato Grosso; PR – Paraná; RJ – Rio de Janeiro; RS – Rio Grande do Sul; SC – Santa Catarina; SP – São Paulo; TO – Tocantins

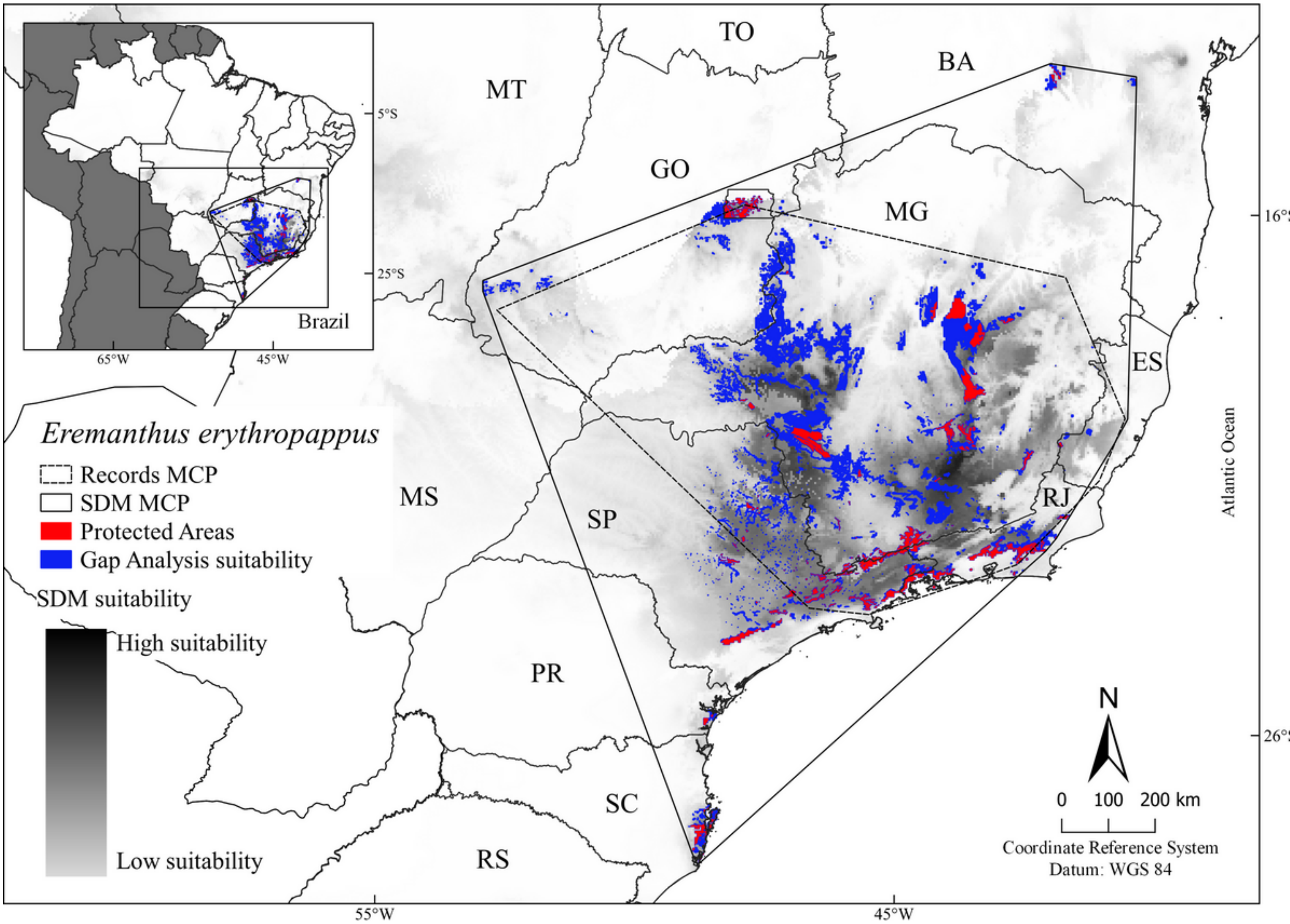

Figure 3

E. erythropappus present time suitability areas and Gap Analysis results. The grey-scale areas show the environmental suitability of Species Distribution Modelling (SDM), with intensity corresponding to the map scale. Darker areas indicate higher environmental suitability. The line involving the environmental suitability area represents the modelling Minimum Convex Polygon (MCP) and the dashed line corresponds to records MCP. The areas suitable for species establishment are in blue and Protected Areas (PAs) are in red. Brazilian states: BA – Bahia; ES – Espírito Santo; GO – Goiás; MG – Minas Gerais; MS – Mato Grosso do Sul; MT – Mato Grosso; PR – Paraná; RJ – Rio de Janeiro; RS – Rio Grande do Sul; SC – Santa Catarina; SP – São Paulo; TO – Tocantins

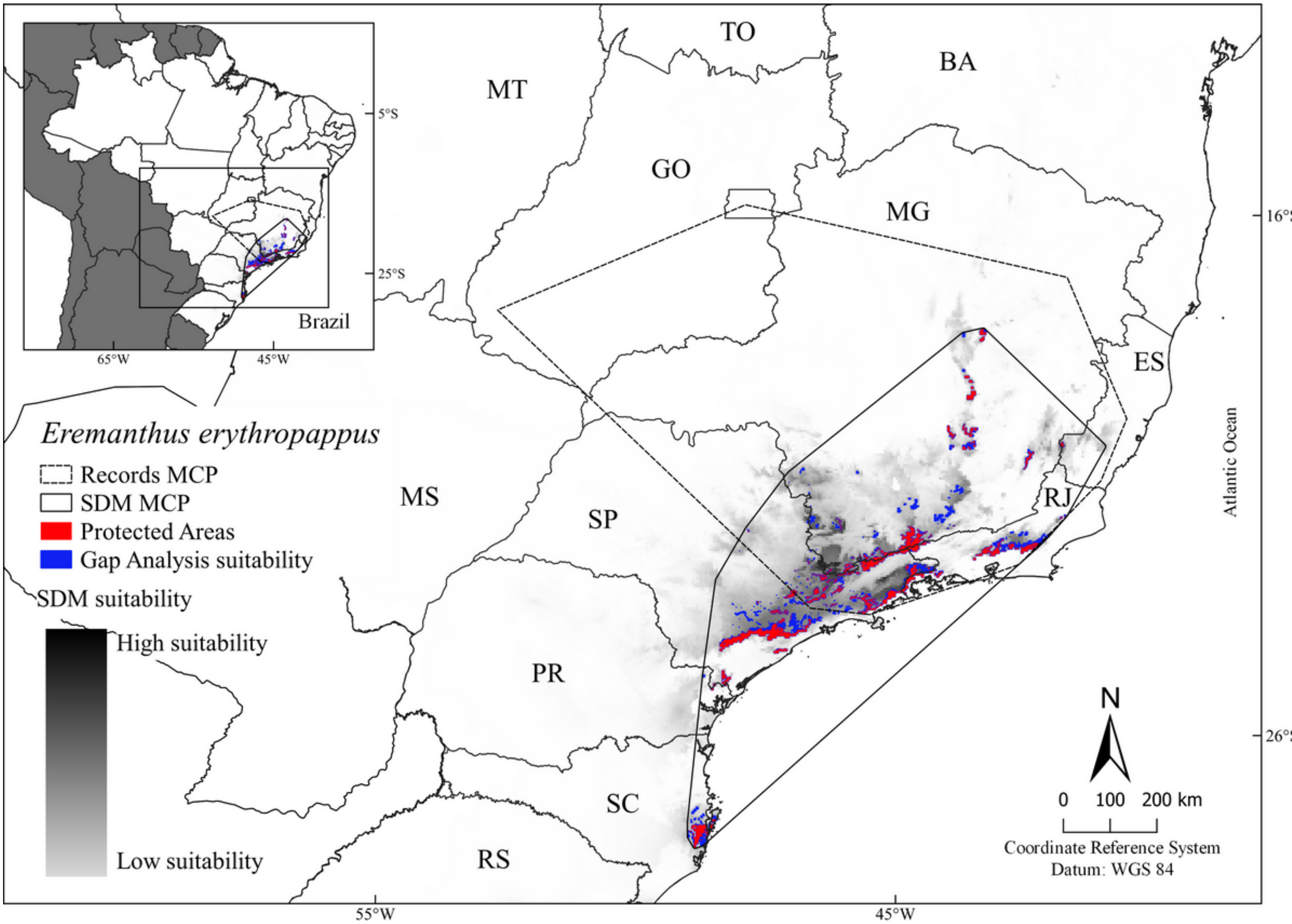

Figure 4

E. erythropappus future (2070 – RCP 8.5) suitability areas and Gap Analysis results. The grey-scale areas show the environmental suitability of Species Distribution Modelling (SDM), with intensity corresponding to the map scale. Darker areas indicate higher environmental suitability. The line involving the environmental suitability area represents the modelling Minimum Convex Polygon (MCP) and the dashed line corresponds to records MCP. The areas suitable for species establishment are in blue and Protected Areas (PAs) are in red. Brazilian states: BA – Bahia; ES – Espírito Santo; GO – Goiás; MG – Minas Gerais; MS – Mato Grosso do Sul; MT – Mato Grosso; PR – Paraná; RJ – Rio de Janeiro; RS – Rio Grande do Sul; SC – Santa Catarina; SP – São Paulo; TO – Tocantins

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